7.73
L868

Los Angeles County Museum

CONTRIBUTIONS IN SCIENCE

BER 57 NOVEMBER 16, 1962

A MORPHOLOGICAL COMPARISON OF *PHOLISMA ARENARIUM* Nuttall AND *PHOLISMA PANICULATUM* Templeton (Lennoaceae)

By BONNIE C. TEMPLETON

SMITHSONIAN NOV 30 1962 LIBRARY

Los Angeles County Museum • Exposition Park • Los Angeles 7, Calif.

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Los Angeles County Museum. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientists and scientific institutions on an exchange basis. Copies may also be purchased at a nominal price.

INSTRUCTIONS FOR AUTHORS

Manuscripts for the LOS ANGELES COUNTY MUSEUM CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information and the form in which it is presented. Priority will be given to manuscripts by staff members, or to papers dealing with specimens in the Museum's collections. Manuscripts must conform to CONTRIBUTIONS style and will be examined for suitability by an Editorial Committee. They may also be subject to critical review by competent specialists.

MANUSCRIPT FORM.—(1) The 1960 AIBS Style Manual for Biological Journals is highly recommended as a guide. (2) Typewrite material, using double spacing throughout and leaving ample margins, on only one side of $8\frac{1}{2} \times 11$ inch standard weight paper. (3) Place tables on separate pages. (4) Footnotes should be avoided if possible. (5) Legends for figures and unavoidable footnotes should be typed on separate sheets. Several of one kind may be placed on a sheet. (6) Method of literature citation *must* conform to CONTRIBUTIONS style—see number 50 and later issues. Spell out in full the title of non-English serials and places of publication. (7) A factual summary is recommended for longer papers. (8) A brief abstract should be included for *all* papers. This will be published at the head of each paper.

ILLUSTRATIONS.—All illustrations, including maps and photographs, should be referred to as "figures." All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Permanent ink should be used in making line drawings and in lettering (do not type on drawings); photographs should be glossy prints of good contrast. Original illustrations will not be returned unless specifically requested when the manuscript is first submitted. Authors may also request their engravings at this time.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. *Changes* after the paper is in galley will be billed to the author. Unless specially requested, page proof will not be sent to the author. 100 copies of each paper will be given free to a single author or divided equally among multiple authors. Orders for additional copies should be sent to the Editor at the time corrected galley proof is returned; appropriate forms for this will be included when galley is sent.

David K. Caldwell

Editor

A MORPHOLOGICAL COMPARISON OF *PHOLISMA ARENARIUM* Nuttall AND *PHOLISMA PANICULATUM* Templeton (Lennoaceae)[1]

By Bonnie C. Templeton[2]

A careful study was made of the two species, and a morphological comparison of their inflorescences, stems, leaves, roots, and hosts is presented. The results of this investigation support the evidence that *Pholisma arenarium* Nutt. and *Pholisma paniculatum* Temptn. are two distinct species; the one species differing from the other in the type of inflorescence, floral parts, manner of growth, host relations, and habitats. Because there are two species of Pholisma instead of the one previously assumed, there had been some understandable confusion in the literature as to the type of inflorescence. This investigation further corroborates the spicate type of inflorescence attributed to *Pholisma arenarium* by Nuttall in the original description.

INTRODUCTION

The genus *Pholisma,* Nuttall, (genotype, *P. arenarium* Nuttall, 1844) is one of three genera of parasitic plants, devoid of chlorophyll, belonging to the family *Lennoaceae.* The genus was considered monotypic until 1938 when a second species, *P. paniculatum* was described by Templeton. It is true that as early as 1885 Greene had described another species, *P. depressum,* but this was considered to be a synonym *of P. arenarium* by Rydberg (1914) and by subsequent investigators, although it was once more given recognition by Templeton in 1938.

In 1935, Copeland reported on the floral structure of *P. arenarium* and found the inflorescence was not a spike, as Nutall had described it, but a compact thyrse. However, as will be shown below, it now is clear that Copeland's material was actually *P. paniculatum,* at that time still undescribed. This error has caused some understandable confusion. It is the object of the present paper to rectify this and to present a comparative study of the two species, and point out their differences and relationships.

Pholisma has been written about but little, even compared with *Lennoa* and *Ammobroma,* the other genera of the *Lennoaceae.* The little on record concerning the morphology of this family of plants is due to the work of Solms-Laubach (1869, 1870) and of Suessenguth (1927). More recently, Carlquist (1953) has reported a chromosome number of n = 18 for *Pholisma paniculatum,* but at this date the count for *P. arenarium* has not been done. The chromosome count of n = 18 on *Ammobroma* has very recently been made but not yet reported.

---

[1]From a Master of Science thesis in Botany at the University of Southern California (1947). Appreciation is cordially due Dr. G. R. Johnstone for his advice and encouragement.

[2]Curator of Botany, Los Angeles County Museum.

SMITHSONIAN INSTITUTION NOV 2 1 1962

MATERIALS AND METHOD

The type locality of *Pholisma paniculatum,* the coastal sand dunes at El Segundo, California, provided all the fresh material of this species used in this study. Numerous stations have been reported for *Pholisma arenarium* in Southern California. One habitat, which furnished abundant material of this species, is near Little Rock, southeast of Palmdale, California. In addition to the numerous specimens of *Pholisma* in the herbarium of the Los Angeles County Museum, forty-five herbarium specimens were secured on loan from the herbaria of the University of Southern California, University of California, Los Angeles, Pomona College, Stanford University, California Academy of Sciences, University of California, Berkeley, and the Gray Herbarium at Harvard University. Of the specimens secured from these herbaria, all had been identified as *Pholisma arenarium* Nutt., with the exception of three specimens that were labeled *Pholisma depressum* Greene.

The fresh material was fixed in formalin-alcohol reagent and then embedded in paraffin or in celloidin. The stains most used were combinations of safranin and Harris haematoxylin, safranin and light green, and Harris haematoxylin alone. Harris haematoxylin gave the best differentiation in the vascular bundles. Approximately 300 slides were made from the stained sections.

Repeated field trips, including numerous excavations, were made over a period of three years to the localities mentioned above.

COMPARISON OF SPECIES

RANGE

Pholisma occurs in nearly every county in southern California. Data on herbarium specimens secured for study indicate Morro Bay, San Luis Obispo County, as the northern-most limit of occurrence and thence southward into Baja California, Mexico. No localities were recorded from Ventura and Orange Counties. Although Nuttall, in his original description of *Pholisma arenarium,* cites a more northern locality (Monterey) than that of San Luis Obispo, the northerly limit of distribution remains doubtful until a further collection is made at Monterey. The geographical distribution of the genus obtained from herbarium records follows:

San Luis Obispo County stations: Seaside dunes, Morro Rock (Grinnell); Morro Bay (Ingles); Guadalupe (Purer); San Luis Obispo (Parish).

Kern County stations: Coyote Holes (Hall & Chandler); Mohave (K.C., Coville & Funston, Blanc); Red Rock Canyon (Hart); Warner Pass (Bixby, Coville, Funston).

San Bernardino County stations: Daggett (Brandegee); Kramer (DeWolf); Quail Springs (Munz & Johnston).

Los Angeles County stations: Lancaster (Pringle, Rich); Little Rock (Templeton); Los Angeles (Lyon); Santa Monica (Rivers, Hasse); El Segundo (Cramer, Miller, Pierce, Templeton).

Riverside County station: Gold Coin Mine (Clark).

Imperial County stations: Colorado Desert (Brandegee); Mountain Springs (Nivens, unknown); Mountain Springs Grade (Munz).

San Diego County stations: La Costa (Alderson); Borrego Springs (Brandegee); Mission, San Diego (Parish & Parish, Abrams); San Diego (Cleveland); San Felipe Wash (Eastwood); Sentenac Canyon (Plunkett).

Baja California stations: Cape San Quentin (Greene); Socorro (Brandegee).

Habitat

Pholisma arenarium Nutt., in the area under observation, occurred in very fine sandy loam of the southwestern part of the Mohave Desert. This region is in the Larrea-Yucca (Joshua-tree) belt of the lower sonoran zone. The terrain is fairly flat and well stabilized. Low shrubs and bushes of gray hue are abundant, and include such widely distributed species as *Lepidium Fremontii, Hymenoclea salsola, Salazaria mexicana, Eurotia lanata,* and many others. Characteristic desert herbs abound in the area, and a root-parasitic herb, *Orobanche Cooperi,* has been found growing in close proximity to plants of *Pholisma arenarium.* According to Jepson, *Pholisma arenarium* is parasitic on the roots of six species of plants. But throughout this entire study, and numerous excavations, the root upon which this plant was attached was traced directly to *Hymenoclea salsola.*

Pholisma paniculatum Templeton occurred in stabilized and semi-stabilized sand dunes along the coast from San Luis Obispo County southward. It was found on the slope and crests of hummocks and occasionally in the depressions between the hummocks of the seaward slope of the sand dunes at El Segundo, California. Herbarium specimen data indicate that it may also be found in sandy washes away from the ocean. The plants associated with *Pholisma paniculatum* consist of several short-lived shrubs and an extensive list of herbs. *Abronia latifolia. Mesembryanthemum chilense, Franseria bipinnatifida, Eriogonum parvifolium, Lupinus chamissonis, Croton californicus, Ericameria ericoides,* and *Oenothera cheiranthifolia* form the community inhabited by *P. paniculatum.* At the time Templeton described *Pholisma paniculatum,* it was believed that this species was parasitic on the roots of *Eriogonum parvifolium* and *Croton californicus.* However, in the numerous excavations during this study, it was found attached to roots that were traced directly to *Croton californicus* only, and these have been, in most cases, the adventitious roots of the host (Fig. 1).

Period of Bloom

Pholisma arenarium has a short blooming period compared to that of *P. paniculatum.* In the three years that these species were observed, the plants of *P. arenarium* came up, bloomed and withered in a period of two months—May and June. On one occasion, specimens were collected in the latter part of April, and in another instance, a collection was made as late as the first week in July. *Pholisma paniculatum,* however, was found in bloom as early as the middle of

February and continued blooming through every month from then to the first part of October. The greatest number of plants were found blooming during the months of May, June, July, and August.

HABIT CHARACTERS

Both *Pholisma arenarium* and *P. paniculatum* are fleshy, root-parasitic herbs, with non-chlorophyll, scale-like cataphylls. *Pholisma arenarium* grew on lateral roots of *Hymenoclea salsola* about seven to twelve inches below the surface of the ground, while the stem supporting the inflorescence extended three to four inches above the ground. Flowering shoots appeared above the ground at varying distances from the host; usually from twenty to thirty inches, but occasionally as close as fifteen inches. *Pholisma paniculatum,* however, grew on the adventitious roots, in most instances, rather than on the regular roots of *Croton californicus*. The basal flowers of the inflorescence rested upon the surface of the sand so as to conceal the stem beneath, except at times when the sand had shifted in semi-stabilized dunes (Figs. 8 and 9). This species occurred at distances of twelve to fifty inches from the base of the host plant but in many cases the plants were found growing among lateral branches of the host (Fig. 4). In most excavations, the base of the stem with its coralloid roots was found attached to the roots of the host at depths of twenty-four to thirty inches; the minimum depth was eighteen inches and the maximum, in one instance, was fifty-seven inches.

Growth arrangement of *Pholisma arenarium* was in single file following the line of development of the host root (Fig. 10). Occasionally single plants were found, and as many as sixteen, but the usual number was two to five in a row. The growth arrangement of *Pholisma paniculatum,* however, was in a more or less clustered formation. Early in the growing season single plants appeared, but as the season progressed more and more plants developed around and in close proximity to the first one. Frequently, this species was found growing in compact clumps (Figs. 3 and 4), fifteen to twenty-four inches in diameter; but only when the parasite was found growing up through the maze of branches of the host.

MORPHOLOGY

INFLORESCENCE: *Pholisma arenarium,* according to the original description, has a spicate inflorescence. The illustration accompanying the original description, and reproduced here as Figure 16, depicts a spike-like inflorescence. The non-coastal specimens recently collected and observed in the field (Fig. 11) and the herbarium specimens, were of spike type and identical with the original description and illustration.

The size of the inflorescence varied from 6 to 12 cm. in length and from 3 to 4 cm. in width. The flowers were extremely compact around a central axis. Upon close examination, this axis possessed nodular ledge-like projections in a spiral arrangement. Upon these are set the individual flowers or clusters of flowers. The upper third of the spike bears individual sessile flowers. In the

middle portion, these are intermixed with flowers borne on minute branches which are usually less than 1 mm. long. The lower portion possesses, in most specimens, compact clusters of flowers in various stages of development on minute or very short branches. These branches usually are about 1 to 3 mm. long, but sometimes, in fully developed plants, are as much as 5 mm. long. They appeared to be an elongation of the nodular projection from which each emerged (Fig. 17), becoming slightly broadened at their distal end to form brief receptacles and upon which were supported three to five flowers. The insertions of the flowers, as well as the clusters of flowers, are formed at acute angles with the thick central axis presenting, on the whole, an appressed appearance. Each flower in the spike is subtended by a thick lanceolate bract 7-12 mm. long. The branches bearing the lateral clusters of flowers are also subtended by bracts which are thicker than those of the individual flowers and are from 14 to 20 mm. long.

Although the inflorescence of *Pholisma arenarium* is described as a spike or spicate, Jepson (1925) added "rarely capitate," and in Brewer & Watson, *Botany of California* (1880), the following is cited: "spike at first capitate, at length oblong." Abundant material of this species in nearly all stages of development has been collected in the Palmdale-Little Rock area and none was found to be capitate. The youngest inflorescence collected is about 18 mm. long and 11 mm. wide (Fig. 13), and appears to consist of a spike of appressed bracts and with very few flowers in this stage of formation.

The inflorescence of *Pholisma paniculatum* is broadly convex to broadly conical in shape, usually two to two and a half times broader than long, whereas those of *P. arenarium* are three to four times longer than broad.

After the first inflorescence of *P. paniculatum,* others occurred always closely surrounding the first one. Excavations revealed that these latter inflorescences were panicles at the ends of branches that had developed from the stem of the first inflorescence (Fig. 8). When these inflorescences developed on branches that were formed near the apex of the primary stem, the inflorescences were smaller than the central one and their stems were more slender and were arranged in a manner that formed a compound, corymbose panicle (Figs. 7 and 9). When these inflorescences occurred on branches that had developed from about or below the middle of the primary stem, however, the inflorescences were approximately the same size and with stems about equal in diameter (Figs. 2, 7a and 7b).

A number of inflorescences of *Pholisma paniculatum* were sectioned longitudinally and, in each case, were found to be a compact, corymbose panicle.[3] Each lower branch was successively longer than the one above it and at almost right angles to the central axis (Fig. 7c) so that the whole inflorescence formed a convex panicle. The branches were numerous and in a spiral arrangement

[3]This term is used here to denote a compact, compound raceme which has developed a form resembling that of a corymb. That is, the compound raceme becomes a corymbose panicle by the lengthening of lower branches while the uppermost remain shorter.

around the central axis. Upon careful dissection, these branches were found to be an intermixture of simple and dichotomous branches, the latter appearing more frequently on the lower part of the panicle than on the upper portion. The forking of each branch develops differently. That is, some branches dichotomize near the main axis; in some, about midway; and in others, toward the end of the branches. The main axis ends in a truncate point, on which are crowded very short dichotomous branches, simple branches, pedicellate and sessile flowers (Fig. 7c). Each branch or fork of the branch possesses two rows of flowers on its upper surface (Fig. 18a); the flowers in one row appeared to alternate with those of the other. Each flower is subtended by a narrow lanceolate accuminate bract that is much thinner by comparison than those that subtended the flowers of *Pholisma arenarium*. The bracts, in addition to those that subtend the flowers, are arranged in a spiral formation along the entire length of the branch. The flowers develop near the top on each side of the branch (Fig. 18c) and project upward. On the lower surface, the branch appears to be clothed with bracts (Fig. 18b). Each branch is supported, also, by a bract that is thicker and broader than those that subtend the flowers. In length, the branches vary from less than 1 cm. at the top, to 3 cm. or as much as 5 cm. at the bottom of the inflorescence. In some of the plants observed, the framework of the panicle became loose and much broadened yet possessing, generally, the corymbose-paniculate form (Fig. 7d).

FLORAL PARTS: The first flowers that bloomed in the spicate inflorescence of *Pholisma arenarium* began at the base and then continued opening successively, in a spiral pattern, to the top (Fig. 11). Upon dissection of the inflorescence it was found that the first flower to open in the compact little cluster at the base of the spike was the one nearest to, and appressed against, the central axis (Fig. 12). The other flowers in the cluster were in successive stages of development and only about two-thirds of these ever became fully developed.

The flowers of *Pholisma paniculatum,* however, do not present the same pattern in the inflorescence as those of *P. arenarium* since they appear irregularly scattered. Like those of the latter species, the first flower on the branches of *P. paniculatum* to reach full development is the one nearest the central axis, and instead of being appressed to the main stem they are somewhat appressed to the branch on which they are growing. Following the first blossoms, the remaining buds on the branches develop acropetally. Nearly all flowers eventually reached full maturity.

Corolla: The greatest apparent difference between the corollas of the two species is in the colors. The throat and limb of *P. arenarium* is of a mulberry-purple color with a band of white, less than 1 mm. wide, edging the limb. In *P. paniculatum,* the throat and usually the veining in the lobes of the limb are colored a pale violet; the remainder of the limb is white, which much resembles the surrounding sand of its natural habitat.

The length of corollas of *P. arenarium* is 9-10 mm., occasionally 12 mm.; width usually 3 mm.; limb spread 5 mm. The length of corollas of *P. paniculatum* nearest the central axis is 12 mm. and those towards the ends of

branches, 8 mm.; width usually 2 mm., occasionally 3 mm.; limb spread 5 mm.

Calyx: The calyx of each species consists of linear, slightly spatulate sepals, about 1 mm. wide, densely glandular hairy on the dorsal side and scarcely, if at all, united at the base. The calyx of *P. arenarium* usually possesses seven sepals, rarely six or eight, and are about the length of the corolla tube or four-fifths of the entire length of the corolla. Frequently they extend beyond the rotate limb. The sepals are of pale violet color and of about the thickness of the floral bracts of *P. paniculatum*. The calyx of *P. paniculatum* possesses five sepals but occasionally there are six or seven. They are whitish, thin, and nearly transparent. In length they are much shorter than *P. arenarium,* being about 5-6 mm. as compared to 8 and 10 mm. in those of *P. arenarium.*

Stamens: The two species of *Pholisma* here considered, differ in the number of stamens, form of the anthers, length of filaments, and activity in anthesis. They are alike in that their stamens are inserted in one series at or near the throat of the corolla tube and alternating with the lobes of the corolla, a character which, according to most authors, distinguishes this genus from that of *Lennoa.*

Filaments: In both species the filaments are adnate for almost their entire length. However, *Pholisma arenarium* has a free portion of 1.5 to 2.0 mm., while the free portion of *P. paniculatum* is only about 1.0 mm. in length in each filament. Occasionally pairs of filaments were found united in *P. arenarium.*

Anthers: Pholisma arenarium usually possesses seven anthers, eight in some instances; rarely five or six. The anthers are oblong, nearly truncate at the apex, about 1.5 mm. long by approximately 1.0 mm. wide (Fig. 15b). The anthers are attached to the filaments near the base of the connective. The connective extends nearly the whole length of the anther and does not create a groove on its dorsal side (Figs. 15c and 16e). Before anthesis, a line of dehiscence appears near the margin of the anther and after anthesis the dorsal side remains flat while the two divisions of the ventral side fold together at right angles to the dorsal portion (Fig. 15e). *P. paniculatum* usually possesses five anthers, rarely six or seven. These are 1.5 to 1.75 mm. long, less than 1.0 mm. wide, and ovate-lanceolate in shape (Fig. 14b). The connective extends from the top to about two-thirds the length of the anther and produces a groove on the dorsal side (Fig. 14c). The attachment of the anther to the filament appears, therefore, about halfway between the base and middle of the anther. Before anthesis the line of dehiscence occurs about one-third in from the margin to the central connective. After anthesis the divisions of the dorsal and the ventral sides fold back against each other (Figs. 14d and 14e). It was found in repeated examinations of both species that the anthers occasionally became reflexed after anthesis.

Pollen: The pollen of both species is about 30 micra in diameter and nearly square in form. Those of *P. arenarium* possess a hyaline case with rounded knobs on the corners. Those of *P. paniculatum* appear to have to spine at each corner but when viewed from another angle appear as hyaline ridges.

Pistil: Further differences appear in the pistils of the two species. The over-all length of those of *P. arenarium* is from 5.5 to 7.0 mm. as compared to 7.0 to 10.0 mm. in those of *P. paniculatum.*

The stigma of *P. arenarium* consists of seven to eight plicated lance-shaped lobes bearing margins edged with light-colored semi-transparent collars (Fig. 15a). Before anthesis the lobes are erect, about 1 mm. long, and form a central hollow tube leading down the style. After anthesis, these lobes converge inward closing over the pit (Fig. 16g). The style is 3.5 to 4.5 mm. long and about 1 mm. in diameter. The carpillary strands form seven to eight ribs which become more pronounced as they approach the lobes of the stigma. The style bears the stigma in the throat of the corolla at about the same level as that of the anthers (Fig. 16c). The ovary is at first globose, later developing into a flask-shaped appearance, 2.0 mm. high and 2.5 mm. in diameter (Figs. 15f and 16i). Cross sections of the ovary show eight cells, each partially divided by a partition which extends from the ovary wall to near the center. Each cell contains two ovules, one on each side of the false partition or about sixteen in all.

The stigma of *Pholisma paniculatum* is a capitate structure, at first smooth and convex but later becoming slightly depressed in the center and somewhat three-lobed (Fig. 6). Under the microscope it appears to consist of a semi-transparent, very finely pitted tissue which caps the upper part of the tubular style (Fig. 14a). After anthesis, this capitate stigma contracts into a dense, light-colored knob of about 1 mm. in diameter and 5.5 mm. to 7.0 mm. in length, smooth to faintly five-ribbed. In anthesis, the style projects the stigma 2.0 to 3.0 mm. beyond the anthers, almost reaching the expanded limb (Fig. 6). After anthesis, the style becomes constricted immediately beneath the stigma, turning brown in contrast to the whitish color of the remaining portion of the style. This activity is progressive downward to the ovary. The ovary, at first subglobose but later becoming depressed in the center, is usually about 4.5 mm. in diameter and 2.5 mm. high. In cross section, the ovaries usually contain five locules each with a false partition similar to *P. arenarium.* Each locule contains two ovules, or ten in all. However, not all of these ovules attain maturity. The capsule is distended from the fully developed seeds and when some of the ovules fail to mature, the capsule becomes distorted. Its margin appears five-lobed with an additional crena in each lobe resulting from the two seeds in each locule (Fig. 14f).

Nutlets: The capsule dehisces circumscissilly, leaving a jagged edge along the line of dehiscence, in both species. The seeds or nutlets (called stonelets by some authors, *e.g.,* Gray, 1896; Solms-Laubach, 1870), are black in *P. paniculatum* and brown in *P. arenarium,* somewhat reniform, finely pitted (Fig. 24) and slightly wedge-shaped in cross section.

STEM: The stems of *Pholisma arenarium* are all simple, unbranched, and more or less regularly erect. Their lengths vary from 15 cm. to 30 cm. from their point of attachment on the root of the host to the base of the inflorescence. Their diameters, 15-20 mm. and occasionally 25 mm., are fairly uniform from the base to near the apex and there broadened only slightly (Fig. 13).

As contrasted with the simple unbranched stems of *Pholisma arenarium,* those of *P. paniculatum* are branched either from near the base (Fig. 5) or at varying levels above the middle of the central stem. In many instances, these branches were found to be repeatedly branched. Twenty-seven branches had ultimately developed (Fig. 2) in one such plant, and in another there were fourteen. The usual number of branches, however, was five to eleven. The usual height of the central stem was about 60 cm., occasionally as short as 30 to 45 cm.; infrequently stems were found to attain a height of 1.5 meters. The stems, because of their branching habit, were somewhat divergent.

Underground stem apex: Neither species showed any external evidence of forming an inflorescence in its development from the base to near the surface of the ground. However, upon approaching the surface of the ground, the blunt cylindrical apex of the *P. paniculatum* stem broadened rapidly to form a widely flaring flat-topped end densely surrounded with bracts. The same habit was present in *P. arenarium* except that the growing tip did not form a flat top. Instead, it widened only slightly and the bracts increased in abundance so that the upper end of the shoot appeared as a small, somewhat pointed spike with appressed bracts.

Internal structure of Stems: Externally, the stems of both species appear to be very much alike but in the cross sections they are strikingly different. The diameter of the stem of *P. arenarium* and of *P. paniculatum* used for microscopical study was 15.0 and 14.0 mm. respectively. The cross sections in both instances have an irregular outline due to the formation, departure, and near departure of the cataphylls. The vascular tissues of the stems consist of numerous collateral vascular bundles arranged in the skeletal pattern of a dictyostele. This vascular cylinder, surrounding a large central pith, extends to within 2 mm. of the epidermis, and in a rather uniform ground tissue appearing as parenchymatous cells. All the parenchymatous cells throughout, contain living protoplasts, few to numerous starch grains, and a globular body resembling a nucleus. In all the sections under observation, only one such globular body occurs in each cell, and appear to be in various stages of organization. Under oil emersion, the perfect ones appear to possess the aspect of a nucleus with a nucleolus and nuclear net; while others appear in various stages of disarrangement from the disappearance of the nucleoli to the breaking up of the nuclear net into a granular beaded condition. This disorganized condition may have resulted from some phase of the microtechnical process. Although it is believed that the globular bodies are nuclei, their true nature has not been conclusively demonstrated.

In *Pholisma arenarium,* the ground tissue in which the vascular bundles lie, consists of large parenchymatous cells 120-150 micra in diameter, 300-375 micra in length, and mainly uniform throughout (Fig. 19). Those in *P. paniculatum* are smaller and more compact, being 75-105 micra in diameter and 210-300 micra long (Fig. 20). Fewer intercellular spaces were noted in this species than in the foregoing one. The epidermal cells of *P. paniculatum* are more or less uniformly oblong, 15-20 micra wide, 120-135 micra long, and 15

micra deep. Those of *P. arenarium*, however, are oblong to rectangularly octagonal, 150 micra long, 30 micra wide, and 30 micra deep.

The collateral bundles in the vascular system of *P. arenarium* are broadly oval to ovate and frequently very closely spaced (Fig. 21). The phloem tissue, separated from the xylem by a narrow line of cambial tissue, is exceed only slightly in amount by that of the xylem. The cells of the phloem and xylem possess a somewhat parallel and fairly uniform arrangement. In *P. paniculatum*, the vascular bundles differ extremely from the foregoing species, in form and in the amount of xylem and phloem tissues. The collateral bundles are narrowly elliptical to broadly oblanceolate throughout the entire dictyostele (Fig. 20), and more widely spaced than in the foregoing species. The xylem contains three to four times the amount of tissue possessed by the phloem; it is long, and narrowed to a point towards the center of the stem (Fig. 22), and is separated from the phloem by a wide band suggesting cambial activity—the cells of which are so dense that no distinct cambium can be recognized. In longitudinal sections of both species, the lignified part of the vascular systems appears to consist entirely of strands of tracheids, compact in *P. arenarium* and less so in *P. paniculatum*.

LEAVES: The structures resembling leaves in both species are scale-like leaves or cataphylls. The shortest ones occur at the base of the stem; the longest ones occur about midway between the base and the inflorescence and each successive cataphyll becomes shorter as it approacehs either the inflorescence or the base. They are in spiral arrangement and appressed to the stem, but become partially reflexed after being exposed to the air. The cataphylls of *P. arenarium* vary from broadly linear with an acute apex to linear spatulate. The cataphylls from the middle of the stem up to the inflorescence graduate from 25 mm. to 10 mm. long. But those from the middle to the base of the stem become gradually diminished in length until the lowest ones are from 4-5 mm. long. They were never more than 2-3 mm. in width. The cataphylls of *P. paniculatum* differ from the foregoing species in that they are broadly lanceolate and deltoid to narrow ovate in form, as well as shorter and wider. The lowest leaves are about 5 mm. long and 3 mm. wide. The longest leaves, occurring in the central portion of the stem, are 9-12 mm. long and about 4 mm. wide. Those nearest the inflorescence are 6 mm. long and about 3 mm. wide. In both species, the cataphylls are entire, smooth except for the grandular hairs, and in transverse sections possess variously five, seven and nine vascular bundles without cambium.

ROOT: The roots of both species are of the coralloid type and are comparatively similar. Those at the base of *P. aranarium* form larger, more compact masses with very short branches extending two to three inches away from the main mass. In *P. paniculatum*, however, the coralloid roots are less compact and more widely branched; the branches extend as much as 12-15 inches. From July through October these branches, and the mass at the base as well, gradually disappeared, leaving only a few thick short roots which held the parasite fast to the root of the host (Fig. 5).

INDUMENTUM: Hairiness in varying degree of density pervades all exter-

nal surfaces of both species. All the hairs are glandular tipped, and are in varying lengths depending on the part of the plant they cover. The density of hairs is less on the bracts, branches, peduncles, and cataphylls than on the sepals. The external surfaces of the corolla possess fewer and shorter hairs while those on sepals are longer and greater in abundance than those on any other part of the plant. Also, hairiness is less abundant on the lower portion of the stem than it is above. The hairs of *Pholisma arenarium* are longer and more slender than those of *P. paniculatum.* Their average length is between 450 and 525 micra, and width not more than 30 micra. Most of the hairs contain seven to fourteen cells in addition to the glandular cap (Fig. 23). The cap appears as a depressed dome scarcely broader than the cells composing the hairs. In *Pholisma paniculatum,* the hairs are short and sturdy, averaging 300 micra long and 30 to 45 micra wide. There are usually three to five cells in each hair, sometimes six or seven, in addition to the convex glandular cap which is about twice the width of the cells beneath (Fig. 25). The cells of these hairs, in nearly every instance, appear to telescope into one another.

DISCUSSION

Copeland (1935) considered the flower structure of *Pholisma arenarium* as having a salver-form corolla. However, Nuttall (1844), in the original description, termed it "funnel-form." Solms-Laubach (1870), in his extensive work on *Lennoaceae,* as well as many others (Jepson, 1925; Munz, 1935; Gray, 1878; Brewer and Watson, 1880; etc.), who include this family in their floras, describes the flower as being tubular. A salver-form corolla, as the term is usually interpreted, has a very slender tube with an abruptly expanded flat limb as that of the phlox. The illustration accompanying the original description of *Pholisma arenarium* corresponds to the form of the corollas of this species that have been thus far examined. Also, the photographic illustration (Fig. 6) of the corolla of *Pholisma paniculatum* shows it to be comparatively similar in form to that of *P. arenarium.* Neither of these illustrations, nor the many corollas of the related specimens examined in this study, bear a resemblance to what has been termed a salver-form corolla.

The determination of the types of inflorescences possessed by *P. arenarium* and by *P. paniculatum* has been most difficult because of the complexity of their structure. In the literature, *P. arenarium* is described as having a spike or spicate inflorescence, while *P. paniculatum* is described as having a corymbose panicle. However, Copeland (1935) believed that there had been a misconception in the literature as to the type of inflorescence possessed by *P. arenarium,* and endeavored to show that it was a thyrse. The plant on which he based his study, however, was a single, immature specimen of a species later described as *Pholisma paniculatum* by Templeton (1938).

A spike is of the indeterminate class and is an inflorescence with a more or less lengthened axis along which the flowers are sessile or nearly so, as in plantain. All the specimens of *P. arenarium,* examined in this study, possessed

a spike or spicate (spike-like) inflorescence. The flowers in the upper portion are all sessile; those in the middle portion, microscopically pedicellate; and those in the lower portion are in sessile clusters on minute branches, the whole presenting an overall appearance of a spicate inflorescence. But since the flowers on the lower portion of the spike are clustered on short branches approximately 3 mm. long and are not single as in the upper part of the spike, the whole is here considered a compound spike.

Since a thyrse is a mixed inflorescence or one in which, while the primary ramification is of the indeterminate order, the secondary or ultimate is wholly or partly of the determinate order, the term cannot be applied to the inflorescence of *P. paniculatum* because its secondary ramifications are wholly indeterminate. Copeland's specimen, being immature, may have presented an appearance of the mixed order or thyrse.

Although *Pholisma arenarium* and *P. paniculatum* bear many characters of common relationship, the manner of growth and the structure of the inflorescence, especially that of *P. paniculatum* appear to resemble, very much, those of *Lennoa*. Furthermore, examinations of herbarium specimens of *Lennoa* indicate that more extensive comparative study of all genera of Lennoaceae is needed to establish accurate generic and specific relationships. For instance, *Lennoa* is segregated, generically, from *Pholisma* by the fact that it is supposed to have its stamens in two series. However, in both of the species of *Pholisma* in this study, there occurred anthers that were reflexed, frequently alternating with the ones that were not, and in this manner presented an appearance of being in two series. The question that now remains is, does the condition of reflexed anthers occur in *Lennoa?* If such should prove true, then one would be inclined to agree with Fournier (1869) that *Pholisma* may be a synonym under *Lennoa*.

SUMMARY

The results of the present study are as follows:

1. Each species has a different host: *P. arenarium* grows on *Hymenoclea salsola* T. & G. (Compositae), while *P. paniculatum* grows on *Croton californicus* Muel. Arg. (Euphorbiaceae).

2. Roots of *P. arenarium* are attached to lateral roots of the host while those of *P. paniculatum* usually grow on adventitious roots of its host.

3. *Pholisma paniculatum* occurs in coastal sand dunes from San Luis Obispo County, California, southward and blooms from February to October; *P. arenarium* occurs in more xerophytic habitats of the desert and has a relatively short growing and blooming period of about two months, May and June.

4. The manner of growth of *Pholisma arenarium* is of simple unbranched stems growing in single file following the line of development of the host root; that of *P. paniculatum* consists of few to many stems clustered at the point of attachment on the host root, and the stems branch at various levels.

5. The inflorescence of *Pholisma arenarium* is a compound spike and that of *P. paniculatum* a compact corymbose-panicle.

6. The length of stems of *Pholisma arenarium* is from 15-30 cm.; the diameter, 15-20 or sometimes 25 mm., is fairly uniform from base to apex. Transverse sections show a dictyostele of numerous collateral bundles which approach the epidermis to within 2.5-3.0 mm. *P. paniculatum* possesses stems 30-60 cm. long, and occasionally up to 135 cm.; in diameter they are about 15 mm. at their bases, then broadening upwards to center of stem to a diameter of 25-35 mm. The dictyostele, in this case, approaches the epidermis to within 2 mm.

7. The collateral bundles of *Pholisma arenarium,* in cross section, are broadly oval to ovate and closely spaced. The phloem is exceeded in amount only slightly by xylem. The collateral bundles of *P. paniculatum* are narrowly elliptical to broadly oblanceolate, and frequently widely spaced, throughout the entire dictyostele. The xylem tissue is long and narrowed to a point and contains three to four times the amount of phloem tissue. The cambial tissue of *P. arenarium* consists of a dense narrow band while that of *P. paniculatum* was considerably wider.

8. The ground tissue consists of large parenchymatous cells containing numerous starch grains and globular bodies which appear as nuclei in varying stages of disorganization. The parenchymatous cells are larger in *Pholisma arenarium,* being 120-150 micra in diameter and 300-376 micra long as compared to those of *P. paniculatum* which are 75-105 micra in diameter and 210-300 micra long.

9. The cataphylls attain their greatest length about midway between the base and apex of the stem. Those of *Pholisma arenarium* are about 10-25 mm. long and vary from broadly linear with an acute apex to linear spatulate, while those of *P. paniculatum* are 6-12 mm. long, deltoid and broadly lanceolate to narrow ovate.

10. The corolla in each species is tubular, with a plicately lobed limb, 5 mm. broad; the lobes are equal to the number of stamens and alternating with them. In *Pholisma arenarium* the corollas are 9-10 mm. long and 3.0 mm. wide, limb spread 5 mm.; the corolla lobes and throat mulberry-purple color with lobes edged with band of white about 1 mm. wide. In *P. paniculatum,* the corollas are 8-12 mm. long, 2-3 mm. wide, with limb spread of 5 mm. The throat and veins in the limb are pale violet. The limb, except for the veins, is almost white.

11. The calyx of each species consists of linear, slightly spatulate sepals 1.0 mm. wide, and scarcely, if at all, united at the base. In *Pholisma arenarium,* there are usually seven sepals, frequently eight, rarely six, light violet to white, fairly thick, about 7-9 mm. or four-fifths to as long as the corolla. In *P. paniculatum,* the sepals are usually five, rarely six or seven, pallid violet to white, thin and almost transparent, about 5-6 mm. or one-half to two-thirds the length of the corolla.

12. The stamens, in both species, are in a single series with filaments adnate to the corolla the greater portion of their length, being free only from 1.5-5.0 mm. in *Pholisma arenarium,* and 0.75-1.0 mm. in *P. paniculatum.* In *P. arenarium,* there are usually seven stamens, frequently eight, rarely five or six; anthers oblong 1.5 mm. long and about 1.0 mm. wide, with connective extending nearly its full length and without groove on dorsal side. After anthesis the dorsal portion of the anther remains flat and the ventral portion folds forward. In *P. paniculatum,* there are usually five stamens, rarely six or seven, 1.0-1.75 mm. long and less than 1.0 mm. wide. Anthers ovate-lanceolate; connective two-thirds the length of the anther, pronounced groove on dorsal side. Following anthesis, the free edges of the dorsal and ventral valves completely recurve. The anthers of both species occasionally become reflexed following anthesis.

13. The pistils of *Pholisma arenarium* and of *P. paniculatum* differ in the form of the stigma, the number of locules in the ovary, and in length. Those of *P. arenarium* are 5-6 mm. long, with ovary globose to flask-shape, 2.0 mm. in diameter, 7-8 loculled and usually two ovules in each cavity. The stigma, which projects to the level of the anthers, has 7-8 lance-shaped lobes which are at first erect but later converge. The pistils of *P. paniculatum* are 7-10 mm. long; ovary at first subglobose, but later becoming depressed, about 4.5 mm. in diameter, usually five-loculled with two ovules in each cavity; not all ovules maturing. Stigma projects 2 mm. beyond the anthers, capitate, its tissue finely pitted and semi-transparent, at first convex but later becoming depressed and 3-lobed.

The seeds are brown in *P. arenarium,* black in *P. paniculatum,* somewhat reniform, finely pitted.

14. The indumentum consists of glandular hairs which cover the external surfaces of the calyx, corolla, bracts, cataphylls, and stems. The hairs of *P. arenarium* are generally longer than those of *P. paniculatum,* being 450-525 micra in the former as compared to 300 micra in the latter. In diameter, the hairs of *P. arenarium* are about 30 micra while those of *P. paniculatum* range between 30-45 micra. The hairs of *P. arenarium* contain 7-14 cells while those of *P. paniculatum* have 3-5 cells, sometimes 6-7 cells. The individual cells in the hairs of *P. paniculatum* appear to telescope into one another while those of *P. arenarium* do not and are of uniform diameters throughout. The glandular cell at the apex of each hair is much larger and more convex in *P. paniculatum* than it is in *P. arenarium.*

CONCLUSIONS

The facts in this investigation support the evidence that *Pholisma arenarium* Nutt. and *Pholisma paniculatum* Templeton are two distinct species; the one species differing from the other in its manner of growth, host relations, type of inflorescence, and floral parts.

This investigation further corroborates the spicate type of inflorescence attributed to *Pholisma arenarium* by Nuttall (1844) in the original description.

LITERATURE CITED

Brewer, W. H. and Serano Watson
1880. *Lennoaceae,* pp. 464-465. In Botany of California (Gamopetalae by Asa Gray) Vol. 1. Second Ed. Boston: Little, Brown and Co.

Carlquist, Sherwin
1953. Documented Chromosomes: *Pholisma paniculatum* Templeton. Madrono, 12(1): 31.

Copeland, Herbert F.
1935. Structure of the flower of *Pholisma arenarium.* Am. J. Botany, 22: 366-383.

Croizat, Leon
1943. The concept of inflorescence. Bull. Torr. Bot. Club, 70(5): 496-509.

Drude, O.
1897. Lennaoceae, pp. 12-15. *In* A. Engler and K. Prantl, die natürlichen Pflanzenfamilien, IV. Teil, Leipzig: Wilhelm Engelmann.

Fournier, E.
1868. Sur le genure *Lennoa.* Bulletin Societe Botanique de France, 15: 10-11.

Gray, Asa
1878. Lennoaceae, pp. 50-51. *In* Asa Gray, Synoptical flora of North America 2 (1), Gamopetalae after Compositae. New York: Ivison, Blakeman, Taylor and Co.

Greene, E. L.
1885. Studies in the botany of California and parts adjacent. Bull. Calif. Acad. Sci., 1(4): 179-228.

Hallier, Hans
1924. Uber die Lennoeen, eine zu Linné's Bicornes verirrte sippe der Borraginaceen. Botanischen Centralblatt (Beihefte), 40(2): 1-19.

Jackson, B. D.
1928. A glossary of botanic terms. New York: J. B. Lippencott Co., 479 p.

Jepson, Willis Linn
1925. Lennoaceae, pp. 734-735. *In* Willis Linn Jepson, Manual of the flowering plants of California, Associated Students Store, University of California, Berkeley.

Kunth, C. S.
1825. *Corallophyllum caeruleum,* pp. 275-276. *In* A. von Humboldt and A. Bonpland, Nova genera et species plantarum, Vol. 7.

Munz, Philip A.
1939. A manual of southern California botany. Claremont, California: Claremont Colleges, 642 p.

Nuttall, Thomas
1844. *Pholisma arenarium,* Nutt. Hooker's icones plantarum, 3: 635 (New Series 7).

Ridgeway, Robert
1912. Color standards and color nomenclature. Washington, D.C.: A. Hoen & Co., 43 p., 53 plates.

Rydberg, P. A.
1914. Lennoaceae. North american flora, 29 (1): 19-20.

Solms-Laubach, Hermann Grafen zu
1867-1868. Ueber den bau und die entwicklung der ernährungsorgane parasitischer phanerogamen. Jahrbücher für wissenschaftliche botanik, 6: 509-638.
1869. Voläufige mittheilung über den bau der gruppe der Lennoaceen. Botanische Zeitung, 27: 38-39.
1870. Die familie der Lennoaceen. Naturforschende gessellschaft zu Halle, abhandlungen 11: 119-178.
1873. Lennoaceae, pp. 36-38. *In* A. P. de Candolle, Prodromus systematis naturalis regni vegetalis, Vol. 17.

Suessenguth, Karl
1927. Über die gattung *Lennoa*. Flora oder allgemeine botanische zeitung, 22: 264-305.

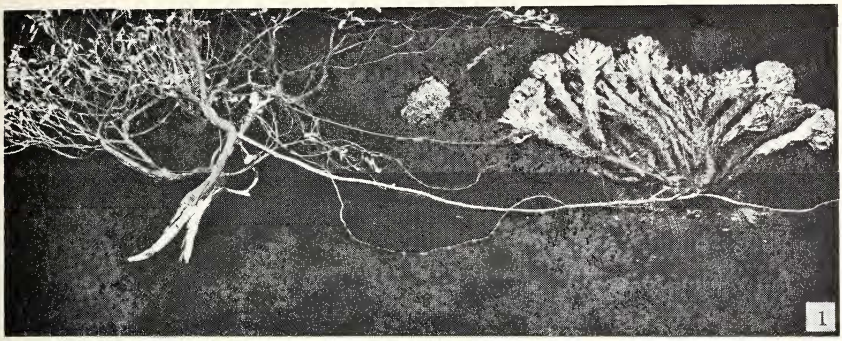
Templeton, Bonnie C.
1938. A new species of *Pholisma*. Bull. So. Calif. Acad. Sci., 37: 98-100.

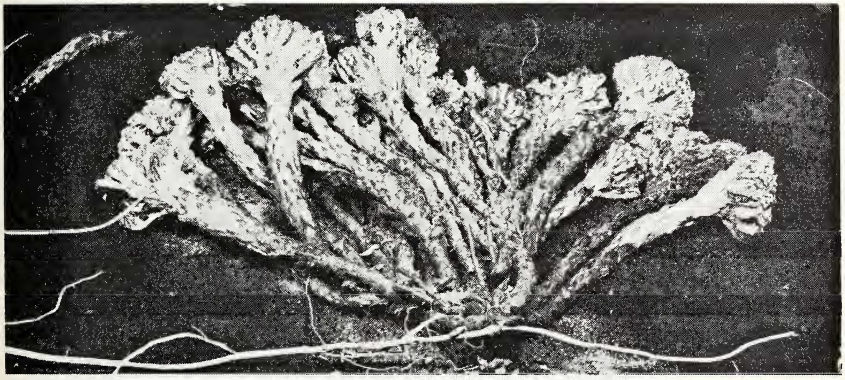
Wilson, Carl L., and Theodor Just
1939. The morphology of the flower. Botan. Review, 2: 97-131.

FIGURES

Note: After this paper had been made up into page proof, the author realized that her magnifications as included in her manuscript figure legends do not correspond to the actual reductions of publication. Therefore, all of the magnifications in these legends should be corrected by a factor of ½.—Ed.

Figs. 1-4. *Pholisma paniculatum* Templeton: Fig. 1. Parasite attached to adventitious root of *Croton californicus* Muell. Arg. In this specimen, twenty-seven branches ultimately were produced by the parasite. Fig. 2. A closer view of the plant showing greater detail in the attachment to the host, the branching of the stems, and of the inflorescences. Fig. 3. A *Pholisma paniculatum* plant partially excavated from sand dune. Fig. 4. A cluster of branches of *Pholisma paniculatum* growing up through lateral branches of *Croton californicus*.


1



3

4

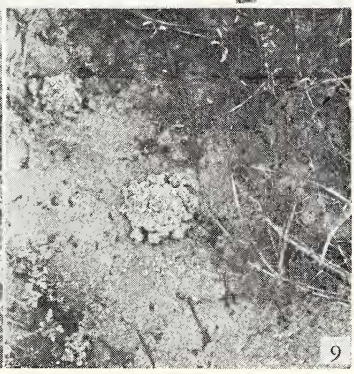
Figs. 5-9. *Pholisma paniculatum* Templeton. Fig. 5. Shows mode of attachment of root of parasite on the adventitious root of host. Note also, the gradual thickening of the stems near the middle, the broad, short, cataphyllary leaves, and the secund arrangement of the flowers on the floral branches (foreground). Fig. 6. External view of flower shows form of corolla, relative length of sepals, and the glandular indumentum. Internal view shows the 3-lobed stigma and its relative position to the anthers. Note, also, that this flower has a short pedicel, whereas, in the following species this structure is lacking. A subtending bract is attached at the base of the pedicel. Fig. 7. Reproduced from the original illustration in the So. Calif. Acad. Sci. Bull., 37:99. (a) Inflorescence taken from a stem that branched near base of plant. (b) Branch removed from central stem midway between inflorescence and base. (c) Longitudinal section through corymbose panicle, showing length and arrangement of branches, and the rows of secund flowers on these branches. (d) Matured, loosely branched panicle. (e) A complete plant showing the manner of branching which frequently occurs near the top of the stem to form a compound corymbose panicle. Fig. 8. Shows clustered habit of growth and form of inflorescences. The largest inflorescence is on the central stem and the surrounding ones are on lateral branches which developed at or below the middle of the central stem. This is the most frequent growth habit. Fig. 9. Top view of plant similar to one illustrated in Fig. 7e.

5

6

a
b
c
d
e
7

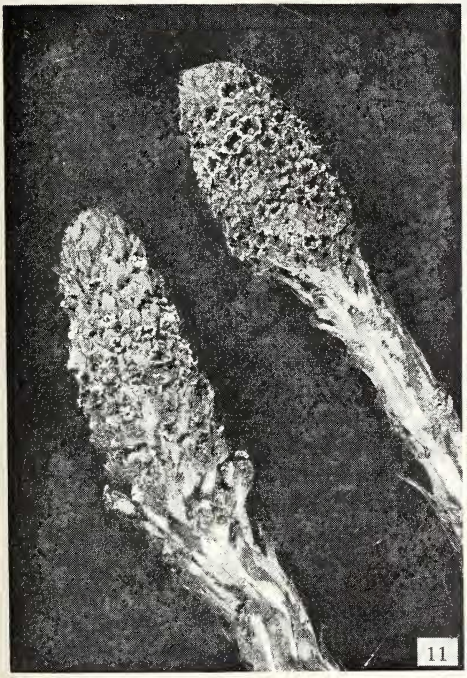
8


9

Figs. 10-13. *Pholisma arenarium* Nutt. Fig. 10. Characteristic habit of growth. Fig. 11. Partially developed inflorescence. Ultimate growth increased its length 25%. Note spiral arrangement of flowers. Fig. 12. Longitudinal section through the inflorescence to show sessile flowers, single flowers with minute branches, and clustered flowers with very short branches. Fig. 13. Young plants of *Pholisma arenarium* on a portion of the lateral root of *Hymenoclea salsola*. Note the simple unbranched stems as contrasted with those of *Pholisma paniculatum*.

10

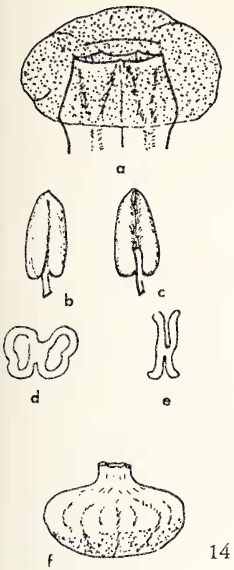
13



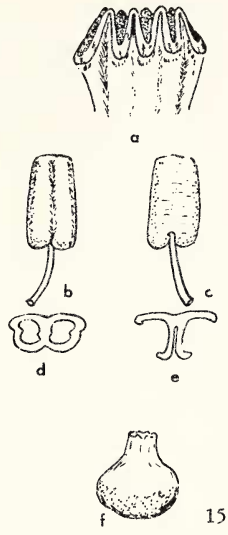
11

12

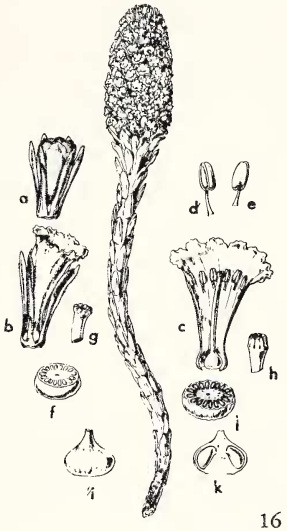
Figs. 14-18. Fig. 14. Parts of the gynoecium and the androecium of the *Pholisma paniculatum* flower. (a) Stigma, about 40x. (b) Stamen, ventral view, 30x. (c) Stamen, dorsal view, 30x. (d) Cross section of anther before anthesis, about 40x. (e) Cross section of anther after anthesis, 40x. (f) Ovary 20x. Fig. 15. Parts of the gynoecium and androecium of the *Pholisma arenarium* flower. (a) Stigma, 40x. (b) Stamen, ventral view, 30x. (c) Stamen, dorsal view, 30x. (d) Cross section of anther before anthesis, about 40x. (e) Cross section of anther after anthesis, about 40x. (f) Ovary, 20x. Fig. 16. Reproduction of *Pholisma arenarium* Nutt. illustrated with original description in Hookers Ic. Pl., Vol. III, New Series VII, p. 626, 1844. (a) Flower before expansion. (b) Perfect flower. (c) Corolla laid open and pistil. (d) Ventral view of stamen. (e) Dorsal view of stamen. (f) Cross section of ovary. (g) Stigma after anthesis. (h) Stigma before anthesis. (i) Immature fruit. (j) Cross section of immature fruit. (k) Vertical section of the same. Fig. 17. View of a small portion of the inflorescence of *Pholisma arenarium* showing the insertion of the flowers on the nodular projections and the external traces of the nodes. Fig. 18. Parts of the inflorescence of *Pholisma paniculatum*. (a) Upper view of dichotomous branch, 2x. (b) View of lower side of a single branch, about 3x. (c) Side view of branch. (d) Flower with one sepal removed to show circumscissle rupturing of corolla and carpel walls. About 6x.



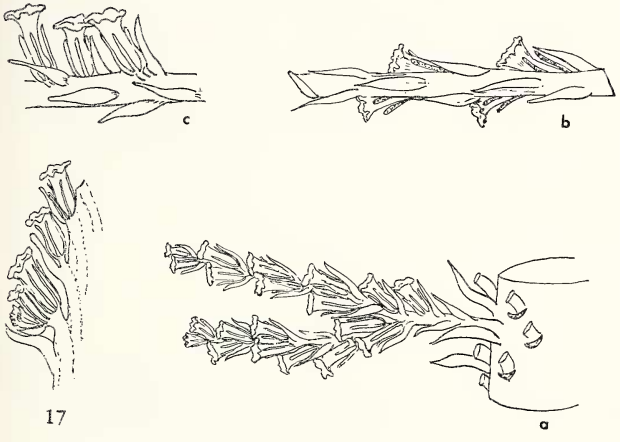
14



15

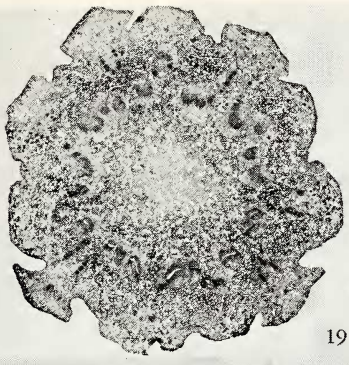


16

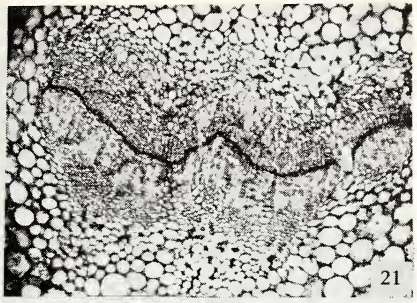


17 18

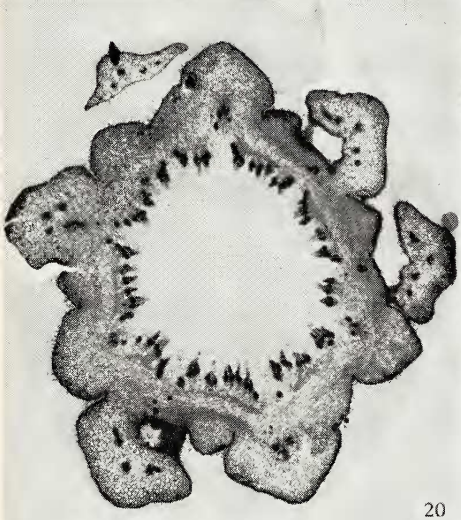
Fig. 19. View of transverse section of stem of *Pholisma arenarium* taken 15 mm. below inflorescence. About 6x. Fig. 20. View of transverse section of stem of *Pholisma paniculatum* taken 15 mm. below inflorescence. About 6x. Fig. 21. Vascular bundles of *Pholisma arenarium*. Note their somewhat oval forms, the narrow dark line which is cambial tissue, and the almost equally proportioned xylem and phloem tissues. About 80x. Fig. 22. Vascular bundles of *Pholisma paniculatum*. Note the meager amount of phloem tissue, the side band of cambial tissue, and the long narrow formation of xylem tissue. About 100x. Fig. 23. Epidermal hairs of *Pholisma arenarium*. Fig. 24. Seeds of *Pholisma paniculatum*. 15x. Fig. 25. Epidermal hairs of *Pholisma paniculatum*.



19



21

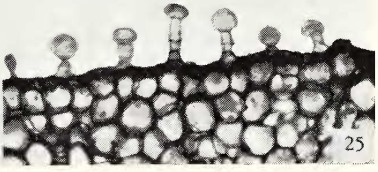


20

22

24

23



25